Carnivora from the Kanapoi Hominid Site, Turkana Basin, Northern Kenya

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ABSTRACT. Kanapoi is the earliest Pliocene site yet described in eastern Africa with a substantial carnivoran record. It includes eight species in as many genera, representing five families. The material is dominated by the hyaenid *Parahyaena howelli* n. sp., but also includes a new *Enhydriodon* species, *E. ekecaman*, the lutrine cf. *Torolutra* sp., the felids *Dinofelis petteri*, *Homotherium* sp., and *Felis* sp., the herpestid *Helogale* sp., and the viverrid *Genetta* n. sp. The Kanapoi Carnivora includes the remains of the first post-Miocene radiation of endemic African Carnivora.

INTRODUCTION

The earliest Pliocene (here taken as ca. 5.2–4.0 Ma) has provided relatively few eastern African localities containing mammalian fossils compared with the million years that followed. Most of the localities that do exist from this time interval have either few carnivores associated with them or are as yet undescribed. Thus, the Apak Member at Lothagam includes only four carnivore taxa (Werdelin, 2003), the Lonyumun Member of the Koobi Fora Formation three (Werdelin and Lewis, unpublished), the Kataboi Member of the Nachukui Formation and Kosia (also West Turkana) also three (personal observations). Outside of Kenya, localities of this time period from Uganda have also yielded few carnivores (Petter et al., 1991). A richer site is Aramis, in Ethiopia, although the carnivores there have yet to be described (Howell, personal communication). Kanapoi, with its somewhat larger sample of carnivores, thus adds significantly to our knowledge of carnivoran evolution in the earliest Pliocene of eastern Africa.

The bulk of the material discussed herein was obtained by the National Museums of Kenya expeditions to Kanapoi in the early 1990s. However, a few carnivore specimens were recovered by the earlier American expeditions. These have been mentioned a few times in the literature under various guises (Behrensmeyer, 1976; Savage, 1978; Howell and Petter, 1980; Turner et al., 1999). In particular, Behrensmeyer (1976) lists *Enhydriodon* n. sp., *Hyaena* sp., and Machairodontinae indet. as present at Kanapoi. Of these, the first is here still referred to *Enhydriodon* Falconer, 1863, the second to *Parahyaena* Hendey, 1974, while the third is here listed as Carnivora indet., as it cannot be determined if the specimen belongs to *Dinofelis* Zdansky, 1924, or *Homotherium* Fabrini, 1890. The remaining taxa described below are new to the Kanapoi fauna.

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CONVENTIONS AND ABBREVIATIONS

Kanapoi fossils in the collections of the National Museums of Kenya are formally accorded the acronym KNM-KP before the accession number; to save repetition, this acronym is omitted from the lists of Kanapoi specimens and abbreviated to KP in the body of the text.

Tooth abbreviations in upper case (I, C, P, M) indicate upper teeth; those in lower case (i, c, p, m) indicate lower teeth. Hence M1 is the upper first molar, p4 is the lower fourth premolar. The following abbreviations are used in the text and tables:

a-p = anteroposterior
Dist = distal
L = anatomical length (long bones); mesiodistal length (teeth)
LpP_4 = length of main cusp of P_4
MC = metacarpal
MT = metatarsal
max = maximum
min = minimum
Prox = proximal
Sust = sustentaculum
transv = transverse
W = buccolingual width
WaP^4 = anterior width (including protocone) of P^4
$WblP^4$ = minimum blade width of P^4

SYSTEMATIC DESCRIPTION

Order Carnivora

Family Mustelidae

Generally speaking, mustelids are rare in the fossil record of eastern Africa. For the most part, this may reflect a preservational bias against smaller species of Carnivora. However, those localities that are particularly rich in smaller Carnivora also differ among themselves in the richness and diversity of their mustelids. Thus, Hadar is rich in small mustelids (personal observations), while Olduvai has fewer taxa, despite the smaller Carnivora being well represented at the latter site (Petter, 1973).
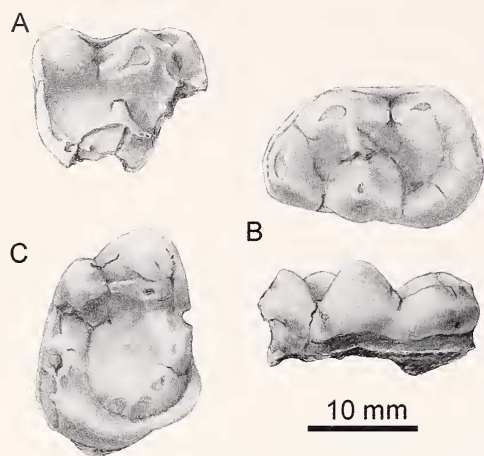
Figure 1 *Enhydriodon* n. sp., **A**, KP 10034A, right P4 in occlusal view; **B**, KP 10034B, right m1 in (top) occlusal and (bottom) lingual view; **C**, KP 10034C, right M1 in occlusal view. In **A** and **C**, anterior is to the right; in **B**, anterior is to the left

This variation may reflect real differences in paleo-ecology between the sites. Nevertheless, the majority of mustelids found in the eastern African fossil record are larger species of the genera *Mellivora* Storr, 1780, *Enhydriodon* and *Torolutra* Petter, Pickford, and Howell, 1991. Kanapoi is no exception to this pattern, with both of the latter genera represented.

Enhydriodon Falconer, 1863

The genus *Enhydriodon* encompasses a number of species of Enhydrini (sea otters) of large to very large size. The genus is known from the Siwaliks of Pakistan and India, where it was first described (Lydekker, 1884; Willemsen, 1992). However, the main diversity within *Enhydriodon* is found in Africa, with several species of varying size known from a number of localities dating between ca. 6.0 Ma (Lukeino Formation; Pickford, 1978) and ca. 2.5 Ma (Omo, Shungura Formation Members E+F; Howell and Petter, 1976). The Kanapoi material represents one of the earlier members of this lineage.

Enhydriodon ekecaman sp. nov.
(Figure 1)

Enhydriodon n. sp. Behrensmeyer, 1976
Enhydriodon pattersoni Savage, 1978 (nomen nudum)
Enhydriodon pattersoni Turner, Bishop, Denys, and McKee, 1999 (nomen nudum)

DIAGNOSIS. Differs from Siwalik *Enhydriodon* in its smaller size. Differs from *E. africanus* Stromer, 1931 (the other described African *Enhydriodon*) by having a broader m1 with a more open talonid basin and relatively smaller paraconid, more robust and larger M1 hypocone(s) and more stoutly built P4.

HOLOTYPE. KNM-KP 10034, A = right P4 (Fig. 1A), B = right m1 (Fig. 1B), C = right M1 (Fig. 1C), D = right C). Written documentation regarding the association in the field of these four specimens was provided by Dr. J. C. Barry (in correspondence). Given this information, it is reasonable to assume that all four belonged to a single individual and therefore the entire hypodigm is chosen as the holotype of this new species.

ETYMOLOGY. After the Turkana "ekecaman," meaning fisherman. The diet of this animal was composed at least in part of fish.

KANAPOI MATERIAL. 10034; associated teeth (holotype).

MEASUREMENTS. KP 10034A, buccal length = 16.5; KP 10034B, total length = 21.2, trigonid length = 11.5, talonid length = 9.3, trigonid width = 13.3, talonid width = 13.5; KP 10034C, buccal length = 12.1, lingual length = 15.8, anterior width = 19.8, posterior width = 19.0. Measurements defined as in Willemsen (1992).

The right upper carnassial, KP 10034A (Fig. 1A), is missing the protocone and most of the hypocone and posterior shelf. The parastyle is short and low but has a distinct anterior cusp. The paracone is high and much the largest buccal cusp. There are blunt crests leading anteriorly to the parastyle, anterolingually toward the protocone and posteriorly toward the metacone. The latter crest is interrupted by a shallow valley before it meets the metacone. The latter cusp is set far posteriorly and is much lower and smaller than the paracone. There was an extensive basin formed posterobuccally to the hypocone and the posterobuccal corner and posterior margin of the tooth lie at nearly right angles to the anteroposterior axis of the tooth. The cingulum extends along the entire preserved part of the tooth except for the posterobuccal corner.

The right lower carnassial, KP 10034B (Fig. 1B) is low, broad, and stoutly built. The three trigonid cusps are all low and pyramidal with their major axes directed either anteroposteriorly (protoconid, metaconid) or transversely (paraconid). In occlusal view, the paraconid is the smallest of the three cusps but all three are worn down to about the same height. The apex of the paraconid is set slightly lingual to the middle of the cusp and it is also slightly broader lingually than buccally. The apex of the protoconid is set slightly anterior to the middle of the cusp. There is a blunt crest that runs down the lingual side of this cusp toward the talonid, making the cusp almost diamond-shaped, though with a gently curved buccal side. Anteriorly, the protoconid is separated from the paraconid by a shallow valley. Posteriorly, the accessory protoconid cusp is very weakly developed, merely forming a low bulge on the posterior face of the cusp. The metaconid is set slightly posterior to the protoconid. Its apex is at the middle of the cusp. The

cusp is triangular in occlusal view, with the apex of the triangle directed toward the buccal side. Anteriorly, the metaconid is separated from the paraconid by a deep valley. Between the trigonid cusps is formed a shallow, flat basin that is about 3 mm wide and 2 mm long. The talonid basin is low and wide. The entoconid is well developed but low. In occlusal view, it is about the size of the paraconid. None of the other talonid cusps is well defined. Instead, they form a low, broad, gently undulating ridge surrounding the central basin. The buccal cingulum is strong and extends from the anteriormost part of the tooth to the posterior end of the hypoconid.

The right M1, KP 10034C (Fig. 1C), is broad, low, and robust, with a very broad lingual basin. The paracone is small, and buccal to it, there is a large parastyle, which is in fact larger than the paracone itself. The paracone is low and worn and connected to the metacone by a narrow valley. The metacone is considerably higher and larger than the paracone and has a pyramidal base. It is set at the posterior margin of the tooth. Lingual to the metacone and separated from it by a narrow valley there is a metaconule that is almost as large as the metacone itself. This cusp is also set at the posterior margin of the tooth. Lingual to the metaconule there is a wear facet for occlusion with m2. This wear facet is confined to the posterior margin of the tooth. At the posterolingual corner of the tooth there is a large swelling of the cingulum, forming a low cusp. The protocone is double, with one cusp set slightly anterobuccal to the other. These two cusps are of about equal size. The cingulum runs around the entire tooth, except anteromedially, where it is worn down by the wear facet for P4, and posterolingually, where the aforementioned m2 wear facet is located. The cingulum is otherwise weakest around the metacone.

The right C, KP 10034D, is short and straight, with a crown that is only slightly longer than it is wide. The tip is worn flat. There is a strong medial cingulum but no lateral one.

DISCUSSION. The material of *Enhydriodon* from Kanapoi is limited, but can nevertheless be distinguished from other African *Enhydriodon* of similar age. The lower carnassial, for example, differs from that of *E. africanus* from Langebaanweg among other features in being shorter and relatively wider, in the somewhat more widely spaced trigonid cusps, and in the flatter and more open talonid basin (cf. Hendey, 1978b). The development of the posterolingual cusplets is more pronounced in the Kanapoi form. The M1 differs from a partial M1 from Kosia (West Turkana, ca. 4.0 Ma) in that the anterolingual corner of the Kanapoi M1 forms a nearly right angle, while the homologous angle of the Kosia tooth is closer to 135 degrees (personal observations). The Kanapoi *Enhydriodon* further differs from younger *Enhydriodon* from formations such as Hadar, Koobi Fora, and Shungura in its much smaller size. Hence, we can infer that the Kanapoi *Enhydriodon* belongs to a hitherto unknown species of that genus, a species that is not at present known from any other site. All four *Enhydriodon* teeth from Kanapoi originate from the American expeditions (1966–72) and were collected in 1967.

Torolutra Petter, Pickford, and Howell, 1991

Torolutra is a genus of otters similar in size to the living European otter *Lutra lutra* (Linnaeus, 1758), or slightly larger. Only a single species, *T. ougandensis*, has been described (Petter et al., 1991). This material is from Nyaburogo and Nkondo in Uganda, while the species has also been tentatively identified from Ethiopia in the Usno Formation of the Omo Group. These localities bracket Kanapoi in age.

cf. *Torolutra* sp.

KANAPOI MATERIAL. 30155, right I3, left and right P4 fragments, premolar fragment, m1 talonid fragment, proximal left radius fragment, proximal right tibia fragment, humerus shaft fragment, partial cervical, thoracic and caudal vertebrae, assorted indeterminate fragments.

The I3 is strongly recurved and has a short crown. The enamel reaches farther down on the lateral than on the medial side. There is a prominent cingulum surrounding this tooth. This cingulum is best developed on the medial side. The root of I3 is relatively straight. The P4 preserves the metastyle, a partial paracone and a part of the lingual protocone shelf. There is no carnassial notch. The protocone shelf is not as long as in *Enhydriodon,* being instead more similar to that of *Lutra* Brisson, 1762. The m1 preserves the posterior part of the talonid, with a prominent hypoconid and low bumps indicating entoconulid and entoconid. The cingulum is prominent around the posterior end of the tooth. The proximal radius fragment is small and broken. The proximal tibia fragment shows only parts of the proximal articular surface. All the vertebrae are relatively robust, the proximal caudal vertebra extremely so, while the cervical vertebrae are relatively much smaller.

DISCUSSION. These specimens compare well, as far as comparisons can be made, with specimens of *Torolutra ougandensis* described by Petter et al. (1991). They are a little larger than the specimens from Uganda, but match the Omo specimens figured by those authors quite well.

Family Hyaenidae

Hyenas are common elements in eastern African Mio–Pliocene faunas. As in Eurasia, there is an extinction event at the end of the Miocene that eliminates the dominant 'dog-like' hyenas that are still present at localities such as Lothagam (Werdelin, 2003). At Pliocene localities, hyenas are mainly represented by relatives of the living hyenas. These Pliocene forms had adaptations to a scavenging life-

style similar to those of living hyenas, but less ac-centuated. At Laetoli, hyenas are abundant, and in-clude fossil relatives of three of the four living hyenas (Werdelin, unpublished). One of these spe-cies is also present at Kanapoi.

Parahyaena Hendey, 1974

There has been some debate regarding the validity of *Parahyaena* as a genus distinct from *Hyaena* (Werdelin and Solounias, 1991; Jenks and Werde-lin, 1998). On the one hand, today these are two monospecific sister taxa, and from this perspective, generic distinction may be deemed unnecessary. On the other hand, the split between the two, as in-ferred from both molecular and paleontological ev-idence, extends down into the Miocene, and most generic splits among carnivores are of about this age or even younger. From this perspective, generic separation is valid. Here I follow the latter path, as I believe that geological age is the only criterion with which to resolve ranking issues when these become critical. Until now, *Parahyaena* was known from the single extant species *P. brunnea* (Thun-berg, 1820), which has a limited distribution and geological age (Jenks and Werdelin, 1998). A single record extends the range of *P. brunnea* into eastern Africa in the middle Pleistocene (Werdelin and Bar-thelme, 1997). This makes the presence of an an-cestral species of *Parahyaena* at Kanapoi highly sig-nificant.

Parahyaena howelli sp. nov.
(Figures 2–5)

Hyaena sp. Behrensmeyer, 1976
Pachycrocuta sp. Howell and Petter, 1980

DIAGNOSIS. Hyaenid of large size (larger than *Hyaena hyaena* Linnaeus, 1758). Mandibular ra-mus robust, premolars moderately developed for bone cracking (weaker than in *Pliocrocuta* Kretzoi, 1938, *Pachycrocuta* Kretzoi, 1938 and *Crocuta* Kaup, 1828). Masseteric fossa clearly subdivided by a ridge into a ventral and dorsal part (unlike *H. hyaena*). Metastyle of P4 clearly longer than para-cone (unlike *Ikelohyaena abronia* (Hendey, 1974) and *H. hyaena*). Metacarpals short and robust (un-like all modern hyenas).

HOLOTYPE. KNM-KP 30235, associated par-tial skeleton (Figs. 2, 3).

ETYMOLOGY. After Dr. F. Clark Howell, lead-ing scholar of African fossil carnivores.

KANAPOI MATERIAL. 10033, complete right mandibular ramus with c–m1 (Fig. 2A, *Hyaena* sp. in Behrensmeyer 1976; *Pachycrocuta* sp. in Howell and Petter 1980); 29249, right mandibular ramus fragment with p4; 29280, proximal fragment of left radius; 29290, right mandibular ramus fragment with p4, distal left radius fragment, right radius shaft fragment; 29293, left distal radius fragment; 29294, right mandibular ramus fragment with p2; 29296, right mandibular ramus fragment with par-tial alveolus for c, alveolus for p2, roots of p3, an-terior root of p4; 29297, left mandibular ramus fragment with roots of p4 and anterior root of m1; 29299, proximal, shaft, and distal fragments of right femur; 29301, left mandibular ramus frag-ment with p4 and anterior root of m1, separate p3; 29302, left P4; 30229, right femur lacking distal end, proximal right tibia; 30234, associated partial left forelimb with left ulna lacking olecranon, left radius, left humerus lacking proximal articulation, left scapholunar, left magnum, left pisiform, left un-ciform; 30235, associated partial skeleton including right mandibular ramus with i2 and c–m1 (Fig. 2B), left distal humerus fragment, right proximal and distal humerus fragments, right radius (Figs. 3A–B), right calcaneum, right tibia lacking distal articula-tion, right ulna lacking distal articulation, frag-ments of the right and left scapulae, left cuboid, right and left navicular, right scapholunar, left lat-eral cuneiform, damaged right lateral cuneiform, right unciform, ?right patella, left MC II lacking distal articulation, right MC II lacking proximal ar-ticulation, proximal part of right MC III, left and right MC V lacking proximal articulations, right MC I, distal part of right MT II, right MT IV lack-ing proximal articulation, left and right MT V lack-ing proximal articulations, proximal, middle and distal phalanges including proximal phalanx of dig-it 1 of the manus, pisiform, sternebrae, and cervi-cal, thoracic, lumbar, and caudal vertebral frag-ments; 30272, associated partial skeleton with right mandible fragment with c, damaged p3, roots of p2 and p4, left mandible fragment with roots of p2–p3, right maxilla fragment with C root, P1 alveolus, nearly complete P2, roots of P3, anterior root of P4, left maxilla fragment with alveolus for I3, dam-aged C, roots of P1–P2, anterior root of P3, right zygomatic, proximal end of right and left scapulae, fragment of distal right humerus shaft, right tibia, proximal, shaft and distal fragments of left tibia, pelvic fragment, left navicular, proximal fragment of left MT V, tuber fragment of left calcaneum, par-tial distal right femur, proximal and distal frag-ments of left femur, fragment of left pisiform, prox-imal end of right MC III, pathological left MT II, distal end of left MT III, right MT III, proximal fragment of right and left MT IV, proximal end of right MT V, proximal phalanx of left manus digit 3, proximal phalanx of right manus digit 4, prox-imal phalanx of right manus digit 5, middle pha-lanx of right manus digit 4, middle phalanx of right and left pes digit 4, middle phalanx of right and left pes digit 5, sternebrae, fragments of cervical, thoracic, lumbar, and caudal vertebrae; 30306, left distal femur fragment; 30463, right mandibular ra-mus fragment with roots of p2–p4; 30482, associ-ated complete left MC III–V (Fig. 4); 30487, prox-imal part of left MT III; 30495, proximal fragment of MT II; 30534, proximal right MT III; 30536, left p3; 30540, right I3; 30541, right lower canine; 30544, left mandibular ramus fragment with p3 and m1, p2 and p4 crowns separate; 31734, prox-

imal right ulna; 31735, proximal left ulna lacking olecranon; 32538, right m1; 32550, left P3; 32552, mandible fragments with associated left c and p3–m1; 32813, proximal right ulna fragment; 32822, left lower canine; 32865, postcranial fragments including a fragment of a proximal MC II, distal metapodials, a distal humerus fragment, and vertebral fragments.

MEASUREMENTS. See Tables 1 and 2

The following is a composite description of the material. The craniodental material shows limited variability, except in size, but where there is variation, this is noted. There is limited duplication between postcranial elements, which allows for a very limited grasp of variation in the taxon, but does mean that a significant proportion of the skeleton of *Parahyaena howelli* is actually known (Fig. 5). Some comparisons with representative morphologies of extant *Hyaena hyaena* are made.

SKULL AND UPPER DENTITION. The skull is represented only by some very small fragments from KP 30272, which unfortunately are too small and damaged to provide any information about the morphology of the species. This specimen has some very damaged teeth and tooth roots that indicate that the upper canine was slightly larger than the lower, that the P1 was small and single rooted, and that P2 was considerably smaller than P3. All these features are normal in hyenas and the only fact of interest is the presence of P1. The I3 is represented by specimen KP 30540, which is worn, but shows the distinctive derived hyaenid subcaniniform morphology of this tooth. The P3 is also represented by a damaged specimen, KP 32550. This tooth probably had a small anterolingual accessory cusp, though damage in this area makes this somewhat uncertain. The main cusp is high and conical, as is typical of derived hyenas, and the posterior accessory cusp is substantial, though precisely how large cannot be determined due to specimen damage. The tooth is similar to P3 of modern *Hyaena*, but the main cusp is larger and stouter. The upper carnassial is represented by the isolated tooth KP 29302. It is typically hyaenid in morphology, with substantial parastyle and protocone, a large and relatively narrow paracone and a long metastyle. The parastyle is robust with a distinct anterior ridge leading down to an anterior cingulum with a hint of a preparastyle. The protocone is large but low and set in line with the anterior margin of the parastyle. The paracone is tall and trenchant and the metastyle long. There is a lingual cingulum that reaches from the posterior root of the protocone to the posterior quarter of the metastyle.

MANDIBLE AND LOWER DENTITION. The mandible and associated material are known from sixteen specimens, most of which are fragmentary and damaged, but include two nearly complete rami, KP 10033 and KP 30235A (Figs. 2A–B). The mandible increases gradually in depth from anterior to posterior and is deepest just posterior to m1. Posterior to this point, the ventral margin of the

mandible rises in a shallow S shape to the angular process. The mandibular condyle is relatively slender in comparison with modern *Hyaena* and consists of two semidistinct areas, a lateral, higher one and a medial, lower one. The latter does not taper medially as is the case in *Hyaena*. The coronoid process is tall and slender compared with that of modern *Hyaena*, and has a distinct backward tilt. The anterior margin of the coronoid process is steeply S shaped. The masseteric fossa is deep and flat. The ventral part (insertion area for the *M. masseter intermedius*) is delimited by a strong ridge and is set distinctly lateral to the more dorsal parts of the masseteric fossa (insertion area for the *M. masseter profundis*). This is in contrast with the situation in *Hyaena*, where the ridge separating these two insertion areas is lower and less distinct and the two areas are located in the same vertical plane. There is a single, large mental foramen situated beneath p2. In KP 10033, the symphysis is broken and all the incisors lost. The lower canine is broken and chipped, but can be seen to have been a relatively robust tooth whose anteroposterior axis is angled relative to the main axis of the ramus. The diastema is of about the same length as in *Hyaena*. The cheek tooth row curves gently to buccal from p2 to p3, then curves gently back from p4 to m1, much as in modern *Hyaena*. Unlike the latter, however, the p2 of KP 10033 is set at an angle to the main axis of the ramus.

The i2 is present only in KP 30235A. It is heavily worn, but is clearly longer (anteroposteriorly) than wide (mesiodistally). The tip is worn flat, though the wear facet is angled from distal (higher) to mesial. On the mesial side, the wear has reached the enamel–dentine juncture. The lingual face is also worn and there is an angle of about 70° between the apical and buccal wear facets. The p2 is the most variable tooth in both size and shape. There is no anterior accessory cusp, but a small swelling at the anterior end of the tooth is present. The main cusp is narrow and conical, with slightly convex anterior and posterior margins. The posterior accessory cusp is low and narrow. The posterior shelf of this tooth is variable in width. In KP 10033, it is narrow in comparison with modern *Hyaena*, which has a small shelf that is not present in this Kanapoi specimen. In KP 30235A and KP 30544, p2 is much broader posteriorly and more similar to the condition in *Hyaena*. In KP 29296, the p2, as judged from the alveolus, must have been noticeably shorter than in the other specimens that preserve traces of this tooth. The p3 has no anterior accessory cusp. Instead, the anterior margin of the main cusp is formed into a low crest that reaches the anterior end of the tooth. The anterior and posterior margins of the robust, conical main cusp are slightly convex. The posterior accessory cusp is low and round and set centrally in a posterior cingulum shelf. The tooth is variable in size and shape, though not to the extent seen in p2. KP 29301 has a p3 that is nearly identical to that of KP 10033,
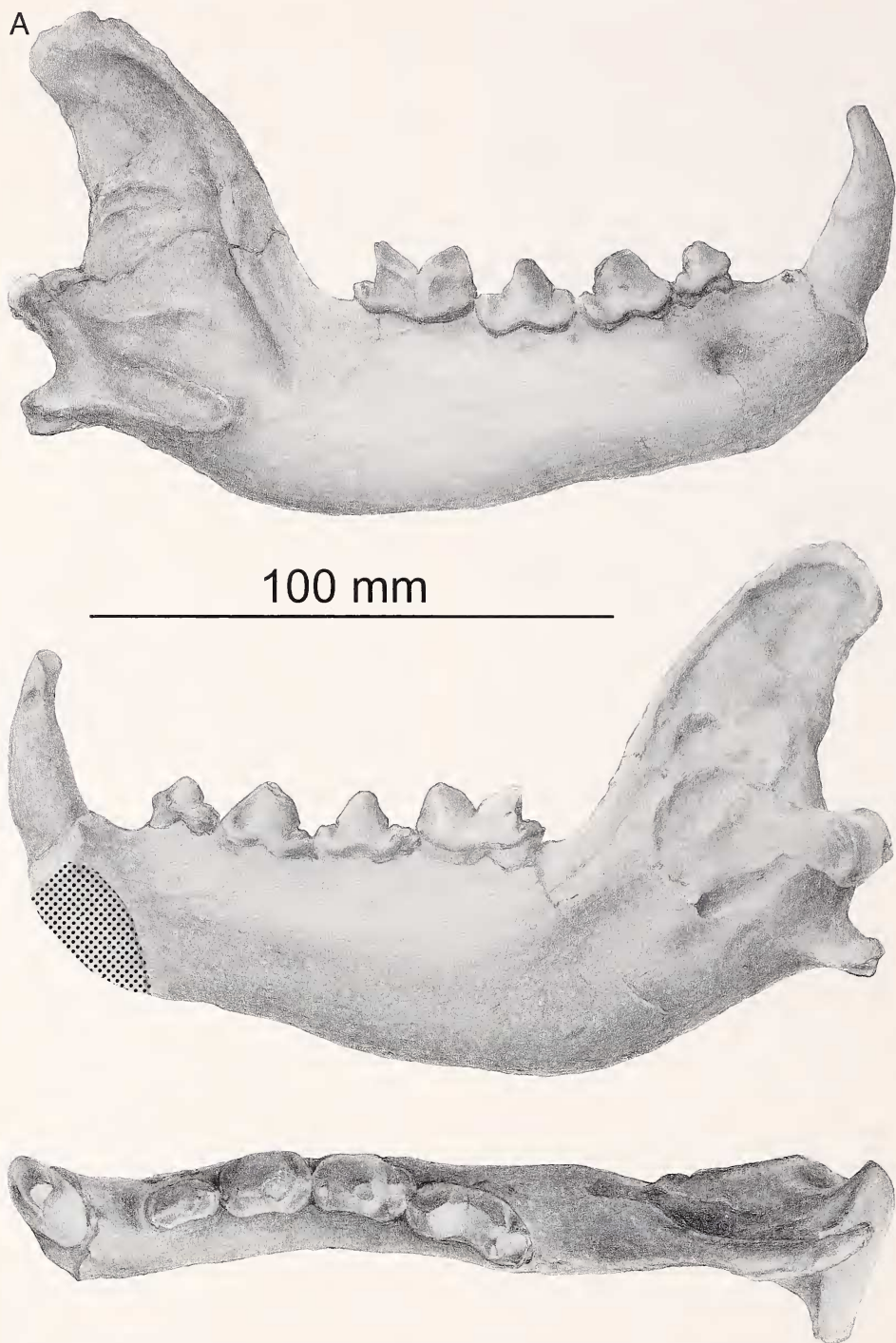
Figure 2 A, *Parahyaena howelli*, KP 10033, right mandibular ramus in (top to bottom) buccal, lingual, and occlusal view; B, *Parahyaena howelli*, KP 30235A, right mandibular ramus in (top to bottom) lingual, buccal, and occlusal view

whereas in KP 30235A and KP 30544, the p3 is narrower and has a more distinct waist. KP 30536 and KP 32552 are intermediate in morphology. The tooth is broadly similar to p3 in *Hyaena* except for the absence of an anterior accessory cusp. The p4 has a small, round anterior accessory cusp appressed to a narrow, conical main cusp with more or less straight anterior and posterior margins. The posterior accessory cusp is relatively high and trenchant. The posterolingual part of p4 has been dam-
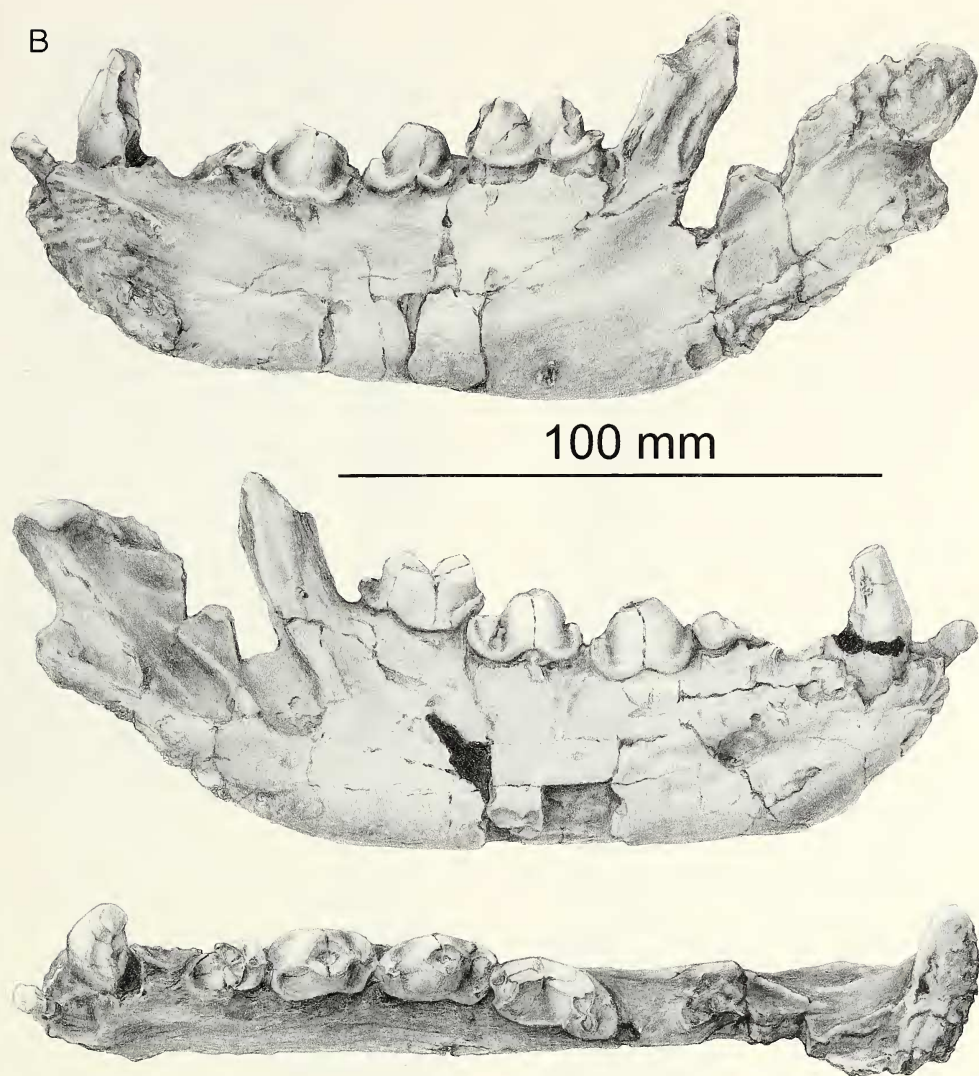
B

100 mm

Figure 2 Continued

aged and it is not possible to determine the width of the posterior part of the tooth. The lower carnassial is long and relatively low. The paraconid is slightly longer and wider than the protoconid. The metaconid is very small but is distinctly developed and the talonid has two cusps, presumably the hypoconid and entoconid. Compared with modern *Hyaena*, the tooth is relatively much longer, the metaconid smaller, and the talonid relatively shorter.

FORELIMB. The humerus is known from KP 30235 (proximal and distal pieces) and KP 30234 (shaft and distal articulation). The proximal fragment is too worn for detailed comparisons with *Hyaena*, but is larger and appears relatively narrower. The distal articulation is transversely broader than in modern *Hyaena*, but is relatively more slender anteroposteriorly. There is a large supratrochlear foramen present in KP 30235.

The radius is known from KP 30235 (Figs. 3A–B) and KP 29280. It is in general very similar to that of *Hyaena*, but is shorter for the same robusticity. The grooves for the *extensor digitis communis, extensor carpi radialis,* and *abductor pollicis longus* are all more deeply incised than in *Hyaena*.

The ulna is known from several fragmentary specimens, KP 30234, KP 30235, KP 31734, KP 31735, and KP 32813. The first two are the most complete and indicate that the ulna of this taxon was slightly shorter but more robust than that of *Hyaena*. The shaft is more rounded than in *Hyaena*, the triceps groove is wider, the ridge on the cranial surface of the olecranon is narrower, the attachment area for the *flexor carpi ulnaris* is less distinct, and the pit beneath the radial notch is shallower. In addition, the rugosity for the articulation with the radius begins more proximally on the

Figure 3 *Parahyaena howelli*, KP 30234, right radius in **A,** anterior and **B,** posterior view

shaft, while the groove for the *abductor pollicis longus* is much more distinct than in *Hyaena.*

Several of the carpals are known from different specimens. The scapholunar is known in specimens KP 30234 and KP 30235AC. It is slightly larger and more slender anteroposteriorly than that of modern *H. hyaena.* Specimen KP 30235AC is broken on the medial side, but in KP 30234, it can be seen that the articular face for the radius extends down onto the medial rim, while in modern *H. hyaena*, there is a much more distinct ridge limiting the radial articulation to the dorsal side of the bone. This may indicate greater mobility of this articulation in the fossil form. In addition, the sulcus

for the *flexor carpi radialis* tendon is deeper and bounded medioventrally by a more prominent ridge than in modern *H. hyaena.* The magnum is known in KP 30234. It is shorter and wider than that of modern *H. hyaena* but is morphologically very similar in all other respects. The unciform is also known from KP 30234. It is more robust than that of modern *H. hyaena* and has a more open articular face for MC III. The pisiform is known from KP 30234. It is larger than that of modern *H. hyaena,* but aside from size is practically indistinguishable from it.

All the metacarpals except MC II are known from complete specimens. MC I, known from KP

Figure 4 *Parahyaena howelli*, KP 30482, associated left MC III–V in dorsal view. Scale = 50 mm

30235P, is a substantial element associated with at least one phalanx. This is corroborated by KP 39235V, which is tentatively identified as the proximal phalanx of the same digit. This phalanx bears a large articular surface for an ungual phalanx, which has not been identified in the material. It is far larger than that of any extant hyaenid, though relatively smaller than its counterpart in *Ikelohyaena abronia* Hendey, 1974, from Langebaanweg, a species that is otherwise smaller than the Kanapoi form. The second metacarpal is known from a distal and a proximal fragment, KP 30235AH and AO, respectively. This metacarpal is more robust than MC II in modern *H. hyaena*. Metacarpals III to V are associated in specimen KP 30482 (Fig. 4) and MC III is in addition known in KP 30235AG and KP 30235BH and in KP 30272. The third metacarpal has larger proximal and distal articular surfaces than MC III in modern *H. hyaena*, while the shaft is more robust but markedly shorter than in the extant species. The plantar side of the proximal articular surface is narrower relative to the dorsal side than in the modern species. The fourth metacarpal is, like the third, shorter and more robust than that of modern *H. hyaena*. The two species are similar in their MC IV morphology, but the proximal articulation in KP 30482 is somewhat more triangular in shape, with a broader dorsal and narrower plantar side than in the modern form. The fifth metacarpal is also more robust and shorter than that of modern *H. hyaena*, the difference being more accentuated in this element. The proximal articular surface with MC IV is set less obliquely and more directly anteroposteriorly than in modern *H. hyaena* and is also very wide compared with the condition in the modern species.

HINDLIMB. The femur is represented by various fragments from specimen KP 30272, including a partial distal femur KP 30272N, proximal fragments of specimen KP 30229, distal fragments, specimen KP 30306, and proximal, shaft and distal fragments, KP 29299. These fragments suggest a femur that is somewhat larger and more robust than the corresponding element in modern *H. hyaena,* but otherwise do not show any distinguishing features of note.

The tibia is known from fragments from the partial skeletons KP 30235D and KP 30272P, Q, as well as from KP 30229. In general, the tibia is not a very diagnostic bone in Hyaenidae and this is true in the present case as well, the fossil specimens only being distinguished from modern *H. hyaena* by their greater size and by the slightly greater development of the medial malleolus of KP 30272Q.

The navicular is known from KP 30235AE and AD, and KP 30272F. This bone is generally similar to that of modern *H. hyaena*, but is slightly larger. It differs in that the plantar process is wider than high, the reverse of the condition in *H. hyaena*. The process for the separation between the articulation with the cuboid and the plantar side of the bone is less prominent than in *H. hyaena*.

The lateral cuneiform is known only from KP 30235BJ and BP. It is larger than the corresponding bone in modern *H. hyaena,* apparently relatively more so than other tarsals and carpals reported here. The proximal articular surface of the fossil is more deeply indented laterally and medially than in *H. hyaena* and, in addition, the distal articular surface (for MT III) is concave in the fossil rather than slightly convex as in *H. hyaena*.

The cuboid is known from KP 30235W. It is the tarsal that differs most from the corresponding element in modern *H. hyaena*. The medial side of the proximal articular surface of the fossil has a medial extension that probably buttressed the medial part of the sulcus for the *M. peritoneus longus* tendon. This sulcus is shallow and nondescript in modern *H. hyaena,* deep and well developed in KP 30235W. The cuboid of *Crocuta crocuta* (Erxleben, 1777), on the other hand, is short and square with a deep, narrow sulcus.

The second metatarsal is known from KP 30495, 30235AM, and 30272AB. The two former are proximal ends that are more robust than MT II in modern *H. hyaena* but otherwise too worn for
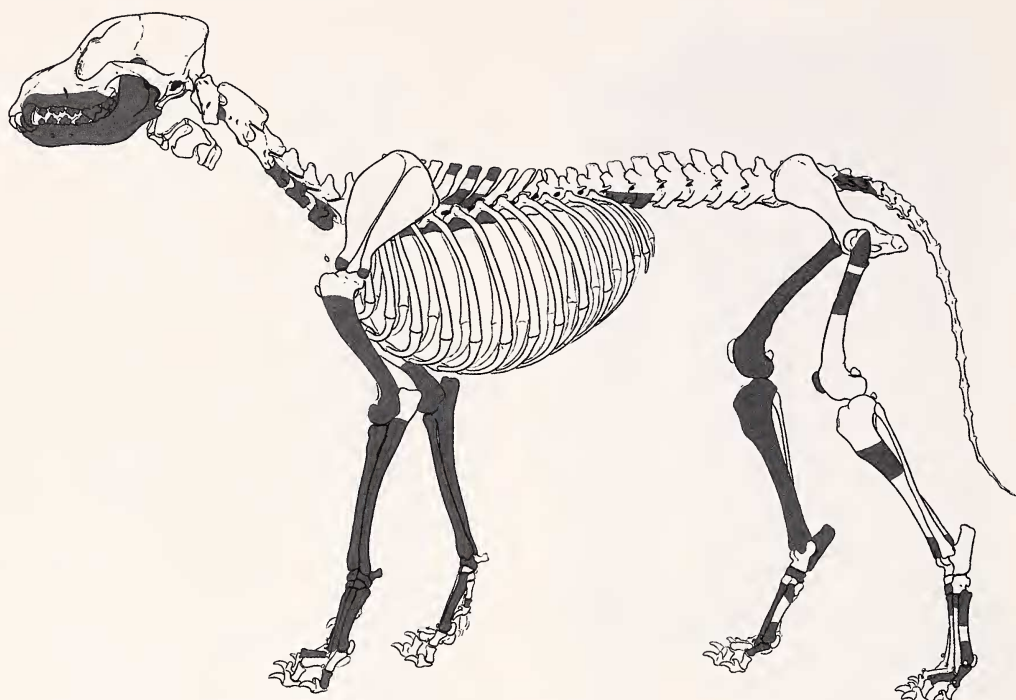
Figure 5 *Parahyaena howelli,* known skeletal parts of *P. howelli* (gray) superimposed on a skeleton of a dog; skeleton adapted from Evans (1993)

meaningful comparisons to be made. The third specimen, KP 30272, is pathological in that the bone appears to have been broken in life and subsequently healed. The distal end of this bone is composed of an amorphous mass of secondary bone suggestive of healing.

The third metatarsal is known from specimens KP 30272U and KP 30272AO, KP 30534, and KP 30487. These specimens are more robust than the corresponding element in modern *H. hyaena,* but are otherwise similar except for the proximodorsal articular surface being concave rather than flat to convex.

The fourth metatarsal is known from KP 30235AF and KP 30272T and AC. It differs from that of *H. hyaena* only in its greater size and in the less expanded proximopalmar eminence.

The fifth metatarsal is known from KP 30235AK and AL and KP 30272AA and KP 30272AP. In this case, the greater size is the only clear difference from extant striped hyaena.

DISCUSSION. KP 10033 was recovered by the American expeditions. It was referred to *Hyaena* sp. by Behrensmeyer (1976) and to *Pachycrocuta* sp. by Howell and Petter (1980). The referral of this species to *Parahyaena* rests chiefly on the length of the metastyle of P4. This is only known from a single specimen, KP 29302, but can also be inferred from the length of the m1 trigonid in relation to p4 and m1 talonid length. The length of

the P4 metastyle is one feature that clearly distinguishes all extant hyena species. *Hyaena hyaena* has a short P4 metastyle, of about the length of the paracone or slightly shorter. In *C. crocuta,* the metastyle of P4 is exceptionally long and straight. In *Parahyaena brunnea,* the metastyle of P4 is longer than that of *H. hyaena* but shorter than that of *C. crocuta.* In the present case, the P4 metastyle has the relative length of that of *P. brunnea.* This contrasts with the condition in *Ikelohyaena abronia,* a possible ancestor of *H. hyaena* (Hendey, 1978a; Werdelin and Solounias, 1991), in which the P4 metastyle is short, as in its putative descendant. No other features contradict assignment of the Kanapoi hyena to *Parahyaena,* and rather than posit the existence of a previously unknown hyaenid lineage, I prefer to suggest a link to the living brown hyena. This represents the first direct indication of the ancestry of the brown hyena, as all other known fossil *Parahyaena* fit comfortably within the extant species (e.g., Hendey, 1974).

Family Felidae

Felids are common elements in the fossil faunas of eastern Africa. Both Machairodontinae and Felinae are present throughout the Plio–Pleistocene, but up to about 1.5 Ma, the former are by far the more common in the fossil record.

Table 1 Dental measurements of *Parahyaena howelli* n. sp.; measurement parameters as in Werdelin and Solounias (1991)

	KP10033	KP30235	KP30541	KP29290	KP29301	KP29249	KP30536	KP32538	KP32822	KP32552	KP32550	KP29302
MLc	12.9		14.0						e15.5			
Wc	10.4	10.9	10.0						e11.0	16.0		
MLp2	13.7											
Wp2	7.9	8.6										
MLp3	18.1	20.0			19.0		19.1			20.3		
Wp3	11.6	11.7			11.7		11.9			a11.9		
MLp4	20.2	21.8			20.4					21.3		
Wp4	11.4	11.7		11.8	11.3	10.9				12.1		
MLpp4	10.0	12.4								11.4		
MLm1	24.3	a25.1								24.5		
Wm1	10.5	11.4						11.8		11.0		
MLrm1	19.9	a20.9						a21.3		19.8		
MLP3											a20.4	
MLP4												34.1
WaP4												18.8
WblP4												9.9
MLpP4												12.0
MLmP4												13.6

a = approximate, e = estimated

Table 2   Postcranial measurements of *Parahyaena howelli* n. sp.

	KP30235	KP30234	KP29280	KP30482	KP30534	KP29293	KP32865
Humerus DistW	46.6	46.1					
Radius L	215.5						
Radius ProxW max	22.3	a21.4					
Radius ProxW min	15.7	16.0					
Radius DistW transv	31.9					32.4	
Radius DistW a–p	20.9					20.7	
MC II ProxW transv					10.6		11.8
MC II ProxW a–p					14.8		14.5
MC III L				91.5			
MC III ProxW transv	13.5			12.5			
MC III ProxW a–p	14.8			15.2			
MC III DistW transv				a14.3			
MC III distW a–p				11.5			
MC IV L				89.3			
MC IV ProxW transv				12.2			
MC IV ProxW a–p				14.6			
MC IV DistW transv				13.6			
MC IV DistW a–p				12.5			
MC V L				75.9			
MC V ProxW transv				18.6 (14.0)			
MC V ProxW a–p				15.6 (13.9)			
MC V DistW transv				15.8 (12.9)			13.1
MC V DistW a–p				11.9			12.3

	KP30272	KP29299	KP30229	KP30235
Femur HeadW		24.3	24.7	
Femur ProxW		51.4	a53.3	
Femur DistW	41.4	a42.4		
Tibia ProxW			44.0	43.7
Tibia DistW	23.9			
Calcaneus Head W transv				14.4
Calcaneus HeadW a–p				20.5
Calcaneus tuber Wmax				20.4
Calcaneus tuber Wmin				11.0
Calcaneus SustW				24.3

	KP30495	KP30487	KP30272
MT II ProxW transv	a9.9		
MT II ProxW a–p	a12.5		
MT III ProxW transv		11.5	10.8
MT III ProxW a–p		17.6	18.3
MT IV ProxW transv			9.8
MT IV ProxW a–p			16.5
MT V ProxW transv			8.2
MT V ProxW a–p			13.1

Dinofelis Zdansky, 1924

Species of the genus *Dinofelis* are among the most common Felidae in the fossil record of eastern Africa. The earliest record there and possibly the earliest anywhere is from Lothagam, where material referred to the genus is known from all members (Werdelin, 2003). The genus is subsequently present at most Plio–Pleistocene sites in eastern Africa until its last occurrence at Kanam East (ca. 1.0 Ma; Werdelin and Lewis, 2001).

Dinofelis petteri Werdelin and Lewis, 2001
(Figure 6)

KANAPOI MATERIAL. 30397, complete right mandibular ramus with c–m1 (Fig. 6); 30542, distal left ulna; ?30429, P4 metastyle.

MEASUREMENTS. KP 30397, Lc = 13.9, Wc = 9.7, Lp3 = 13.1, Wp3 = 7.3, Lp4 = 20.6, Wp4 = 9.7, Lm1 = 23.2, Wm1 = 10.6. Measurement parameters defined in Werdelin and Solounias
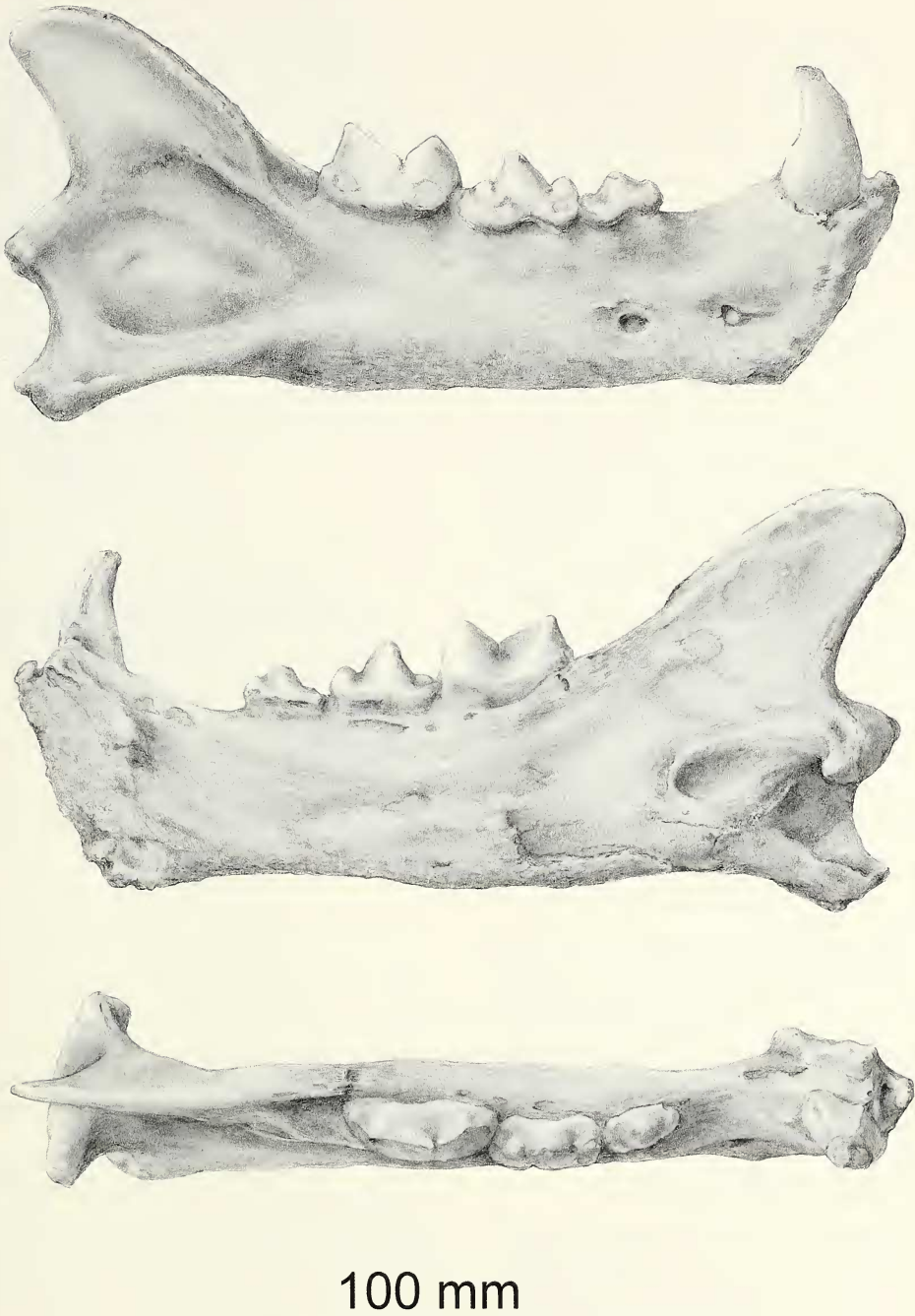
Figure 6 *Dinofelis petteri,* KP 30397, right mandibular ramus in (top to bottom) buccal, lingual, and occlusal view

(1991). The horizontal ramus is low, but broad, with a noticeable thickening of the corpus. The depth is about the same throughout. The symphysis is deep and short and nearly vertically oriented, producing a small anteromedial chin. There are two mental foramina, one below the diastema between the canine and p3 and one beneath the anterior root of p3. Both are set low on the ramus. The masseteric fossa is deep and the masseteric foramen large, while the coronoid process is relatively short anteroposteriorly. The condyle is thickest medially and tapers gradually toward the lateral end. The

angular process is robust and angled ventrally relative to the horizontal ramus.

The space for the incisors is very narrow, suggesting that they were either staggered or very small. The lower canine is short and robust and angled outward with respect to both the anteroposterior axis of the ramus and the sagittal plane. The diastema is long. The p3 has a small anterior accessory cusp, a low, conical main cusp, and a posterior basin that forms the widest part of the tooth but lacks a posterior accessory cusp. The p4 is long and slender. The anterior accessory cusp is well developed and set far anteriorly, well away from the main cusp. The main cusp is triangular with straight anterior and posterior margins. The posterior accessory cusp is similar in size to the anterior but set closer to the main cusp. There is a small posterior cingulum cusp and a low lingual cingulum crest, making the posterior basin the widest part of the tooth. The lower carnassial is typically felid, with a broad paraconid and narrower and somewhat longer protoconid. There is a minute, posteriorly located talonid. The m1 is set in a groove at the posterior end of the horizontal ramus. This groove is bounded laterally by the masseteric fossa wall and medially by the root of the ascending ramus.

The tip of the anconeal process of the ulna is broken and the specimen is somewhat eroded. It is a relatively small, gracile bone compared with later, better known *Dinofelis* (see Werdelin and Lewis, 2001 for a discussion).

DISCUSSION. This and other *Dinofelis* material from Africa and other regions is described and extensively discussed elsewhere (Werdelin and Lewis, 2001). The Kanapoi material is referred to the species *D. petteri*, which is also known from a number of other sites (Allia Bay, Laetoli, Hadar Sidi Hakoma, and Denen Dora Members, Omo Shungura Members B–F, Koobi Fora Tulu Bor Member, West Turkana Lomekwi Member) in eastern Africa. This gives the species a temporal range of ca. 4.2 Ma (Kanapoi) to 2.3 Ma (Shungura Member E/F).

Homotherium Fabrini, 1890

Material that can be referred to *Homotherium* is relatively ubiquitous at eastern African Plio–Pleistocene sites. Unfortunately, much of this material is fragmentary or undescribed. Therefore, the taxonomy of eastern African *Homotherium* is confused. Petter and Howell (1988) described a skull from Hadar as *Homotherium hadarensis,* noting its differences from Eurasian *Homotherium*. On the other hand, Harris et al. (1988) described a skull from West Turkana, tentatively affiliating it with *Homotherium problematicum* (Collings et al., 1976). The latter comparison cannot be maintained, but neither does the West Turkana skull seem to belong to *H. hadarensis*. African *Homotherium* requires renewed investigation for the resolution of these problems.
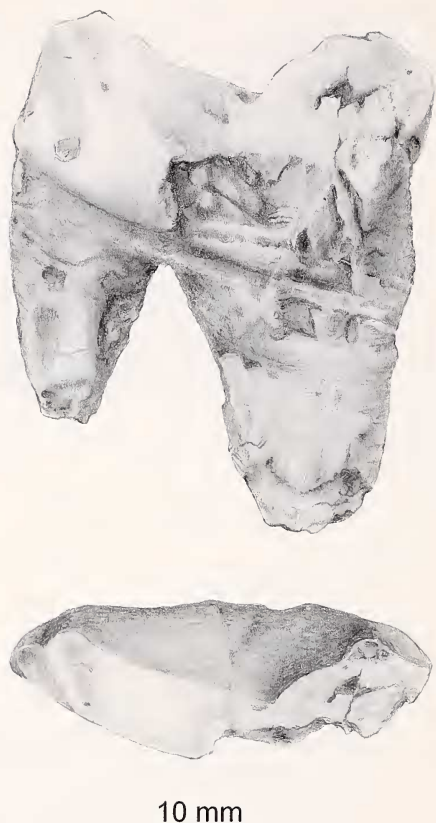

10 mm

Figure 7 *Homotherium* sp., KP 30420, right m1 in (top) buccal and (bottom) occlusal view

Homotherium sp.
(Figure 7)

KANAPOI MATERIAL. 30420, right m1 (Fig. 7); 32558, complete right MC IV; 32820, complete proximal phalanx; 32882, proximal metatarsal fragment.

The lower carnassial is very long and slender. The paraconid is slightly broader than the protoconid, but the latter is the longer of the two cusps. There is no metaconid and no talonid. The shaft of MC IV is relatively straight and quite rounded in cross-section, widest just below proximal articulation and gradually tapering distally. The distal articulation is about as tall as it is wide. The proximal phalanx is large and robust. The shaft is gently arched. The proximal articulation is broad and low, while the distal articulation is more nearly equal in height and width, though the width is still somewhat greater. Rugose surfaces are prominent on the medial and lateral sides of the shaft.

DISCUSSION. All of this material is clearly felid and is too large to represent any taxon other than *Homotherium*. The m1 matches the lower carnassial of most other *Homotherium* in size and proportions, though it is distinctly smaller than m1

from a *Homotherium* mandible from Koobi Fora (KBS Member), as well as that of *H. problematicum* from Makapansgat. However, none of the Kanapoi material can be considered diagnostic among species of *Homotherium* and the material must be left as indeterminate species for the time being. The Kanapoi material represents the hitherto oldest described material of *Homotherium* in eastern Africa.

Felis Linnaeus, 1758

Fossils of the genus *Felis* are very rare in the fossil record of eastern Africa. In fact, aside from the Kanapoi record, only a single specimen from the Denen Dora Member of the Hadar Formation can be unequivocally referred to *Felis sensu stricto* (personal observations).

Felis sp.

KANAPOI MATERIAL. 30546, fragments of P4 of one or two individuals.

This material comes from a small feline, smaller than "*Felis* small species" from Laetoli (Barry, 1987). It is the size of the extant *F. lybica* Forster, 1780. The main cusp is taller and shorter anteroposteriorly than in the Laetoli specimen.

DISCUSSION. Given the fragmentary nature of the material, as well as the almost complete lack of knowledge of fossil African *Felis* at the present time, it is inadvisable to put a specific name to this material.

Family Herpestidae

Apart from the notable exceptions of Laetoli and Olduvai, sites that have been excavated for micromammals, herpestids are rare in the fossil record of eastern Africa. Because of the lack of screen-washed localities, it is not at present possible to establish whether this is a sampling artifact, whether it reflects a biased sample of localities vis-à-vis environment, or whether it is a real phenomenon.

Helogale Gray, 1861

Dwarf mongooses are among the more common herpestids in the Plio–Pleistocene of eastern Africa, with several species described from Laetoli and the Shungura Formation (Wesselman, 1984; Petter, 1987).

Helogale sp.

KANAPOI MATERIAL. 32826, fragments of a right mandibular ramus with broken p4, damaged m1, roots of m2; 31034, lower canine.

This material belongs to a very small carnivore species. The horizontal ramus is slender but relatively deep. In the carnassial, the paraconid is by far the largest and tallest cusp, making up about half of the trigonid in occlusal view. The protoconid is small and set buccally. The carnassial notch is relatively shallow. The metaconid is set directly

behind the paraconid and lingual to the protoconid. It is separated from both by shallow valleys. The talonid is low and short. The hypoconid is prominent, the entoconid less so. The m2 is single rooted, while the p4 is too damaged to provide any useful morphological information.

DISCUSSION. To the extent that comparisons can be made, this material strongly resembles *Helogale* species. It is a little larger than *H. palaeogracilis* (Dietrich, 1942) from Laetoli by the same amount that that species is larger than the extant *H. hirtula* (Thomas, 1904). The Kanapoi material clearly is not adequate for specific identification, and I prefer to leave it as *Helogale* sp. herein.

Family Viverridae

Viverrids are not uncommon in the Plio–Pleistocene of eastern Africa, but very little of the material has as yet been published. However, most of the material pertains to species larger than any living viverrid. Such species are found in three lineages, *Viverra* Linnaeus, 1758, with *V. leakeyi* Petter, 1963, known from a number of localities, *Pseudocivetta*, with the single species *P. ingens* Petter, 1973, of uncertain affinities, and a third species from Koobi Fora that may be related to *Civettictis* (Petter, 1963, 1973; Hunt, 1996). Smaller viverrids are less common, and almost none of the material has been studied.

Genetta Cuvier, 1816

Genetta sp. nov.
(Figure 8)

Material that can be referred to *Genetta* is known from a number of localities in the Plio–Pleistocene of eastern Africa. Kanapoi is the oldest of these, though material referred to cf. *Genetta* (two species) is known from Lothagam (Werdelin, 2003). Younger localities with material of *Genetta* sp. include Laetoli and the Shungura Formation, members B and C. The first record of the extant *G. genetta* (Linnaeus) is from the Upper Burgi Member of the Koobi Fora Formation (personal observations).

KANAPOI MATERIAL. 32565, left maxilla fragment with posterior half of P3 and complete P4–M1; 32815, left mandibular ramus fragment with m1 and roots of p4 and m2 (Fig. 8); 30222, left lower canine.

The maxilla fragment represents a small carnivore species. The P3 is damaged anteriorly. It has a small but relatively tall posterior accessory cusp. The upper carnassial is elongated, with a small but sharp parastyle. The protocone is large and reaches further anteriorly than the parastyle. It is separated from the paracone by a deep valley. The paracone is large but short and pyramidal in shape. The metastyle is long and low, longer than the paracone. The M1 is broad but short and set at about 60° to P4. The parastyle wing is large and well developed,
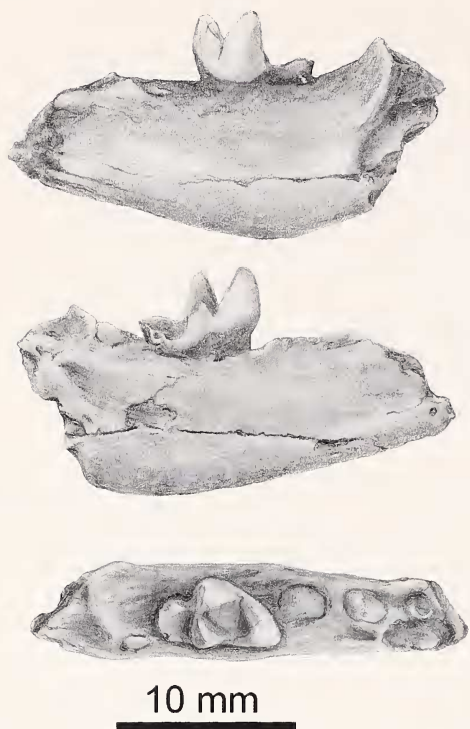
Figure 8 *Genetta* n. sp., KP 32815, left mandibular ramus fragment in (top to bottom) buccal, lingual, and occlusal view

while the metastyle wing has been reduced. Both the paracone and the metacone are present, with the paracone being the larger of the two. The tooth tapers gradually in length to the protocone, which is the largest single cusp of the three cusps on M1. There is a deep basin between the paracone–metacone and protocone.

The horizontal ramus of the mandible is fairly thick and deep, becoming deeper but thinner at the level of the ascending ramus. The masseteric fossa reaches to the posterior end of m1. The lower carnassial has a trigonid with tall cusps and a short, narrow talonid. In occlusal view, the paraconid is the largest cusp, but the protoconid is taller. The long axis of the paraconid is set at nearly right angles to the main axis of the tooth. The carnassial notch is deep, while the notch separating the paraconid from the metaconid is shallower but wider. The paraconid–protoconid shearing blade is set at about 45° to the main axis of the ramus. The protoconid is set buccally, overhanging the ramus to some extent. The metaconid is set directly posterior to the paraconid and lingual to the posterior end of the protoconid. It is separated from the protoconid by a shallow transverse valley. The talonid is very low and short compared to the trigonid. There are two distinct cusps, which can be homologized with the entoconid and hypoconid. The m2 was small and single rooted.

The lower canine KP 30222 is small and recurved. The root is robust and relatively straight, though broken off part way down. The crown shows no accessory cusps or grooves.

DISCUSSION. The morphology of the teeth readily identify these specimens as belonging to the genus *Genetta*. They are similar in size and most features to the extant *G. genetta,* but there are differences that indicate that the Kanapoi material represents a separate species. These differences include the less reduced protocone, broader P4 blade, and less reduced M1. These are all features in which the extant *G. genetta* is more derived than the Kanapoi form.

Carnivora Family Indet.

The following specimens have not been identified to family, mainly because of their incomplete nature. In view of the relative abundance of the species in the identified material, it seems likely that most, if not all, the material of "medium species" should probably be referred to *Parahyaena* sp. nov. 29289, distal metapodial fragment, medium species; 32827, proximal phalanx, medium species; 32517, distal fragment of left? MC V?, small species (may not be carnivore); 32549, proximal metapodial fragment (may not be carnivore); 31738, distal metapodial fragment, medium species; 32808, proximal phalanx, medium species; 32569, fragment of anterior premolar, possibly P1, medium species; 32540, left lower canine, small species (possibly mustelid); 478, fragment of astragalus, large species (Machairodontinae indet. in Behrensmeyer 1976); 30478, vertebral fragments and distal metapodial fragment, medium species; 30494, vertebral centrum; 32883, vertebral fragments including dens of axis, medium species; 30432, distal right humerus condyle; 29291, fragment of distal left femur; 30469, fragment of proximal left femur; 29298, right upper canine.

SUMMARY

The Kanapoi carnivore fauna, with its eight species in as many genera, representing five families, is a substantial addition to the early Pliocene record of Carnivora in Africa. It shares a number of genera and species with other African early–middle Pliocene localities, such as Langebaanweg and Laetoli, but overall has a unique mixture of species. Similarities with Langebaanweg, which is somewhat older and relatively distant, are at the generic level (*Enhydriodon, Dinofelis, Homotherium*), while similarities with Laetoli, which is closer both in age and geography, lie at the species level (*Parahyaena howelli, D. petteri*). The small number of taxa from the Apak Member at Lothagam makes comparisons with that site difficult.

On the other hand, differences between Langebaanweg and Kanapoi show that the former still includes Miocene relicts (taxa such as *Hyaenictis* Gaudrey, 1861, *Plesiogulo* Zdansky, 1924, and

Machairodus Kaup, 1833), while the latter is more typically Pliocene and lacks these Miocene forms.

The Nawata Formation at Lothagam includes a number of forms whose affinities lie outside Africa (mostly in western Eurasia, but also on the Indian subcontinent). The Kanapoi fauna, on the other hand, includes only forms whose immediate forebears can be found in Africa. Thus, the Kanapoi fauna represents the currently best-known evidence for the first post-Miocene radiation of endemic African Carnivora.

ACKNOWLEDGMENTS

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